REVIEW OF THE NEW WORLD TREEHOPPER TRIBE STEGASPIDINI (HEMIPTERA: MEMBRACIDAE: STEGASPIDINAE): I: BOCYDIUM LATREILLE, LIRANIA STÅL, AND SMERDALEA FOWLER

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Abstract.—The tribe Stegaspidini Haupt, 1929 (Hemiptera: Membracidae: Stegaspidinae) and three included genera, *Bocydium* Latreille, *Lirania* Stål, and *Smerdalea* Fowler, are described and illustrated based on adult and nymphal morphology. *Bocydium* has 15 valid species, including **B.** *duoglobum* **Cryan**, **new species**; *Lirania* is monotypic; and *Smerdalea* has 4 valid species, including **S.** *imminens* **Cryan**, **new species**. The genus *Smerdalea* is transferred from the tribe Microcentrini to Stegaspidini; a description of the previously unknown nymph of *S. elevata* Cryan is given. Updated taxonomic keys for the tribe and for the genera *Bocydium* and *Smerdalea* are presented; complete species checklists are compiled, with synonymies, for each genus.

Key Words: Membracidae, Stegaspidini, Bocydium, Lirania, Smerdalea, taxonomy

Stegaspidini are unusual and often conspicuous treehoppers occurring in Mexico and throughout Central America and most of South America. Here included in this tribe are the genera Bocydium Latreille, Lirania Stål, Smerdalea Fowler, Lycoderes Germar, Oeda Amyot and Serville, Stegaspis Germar, Flexocentrus Goding, Stylocentrus Stål, and Umbelligerus Deitz. Whereas all members of its sister tribe Microcentrini are solitary as adults (Cryan and Deitz, in press), some stegaspidines have been observed in small aggregations of adults and nymphs (Haviland 1925a, Boulard 1979g). In addition, species of Flexocentrus, Stegaspis, and Lycoderes have been observed with ant attendants (Cryan and Deitz, in preparation). Host records currently available for Stegaspidini are restricted to the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae.

The primary goal of this work is to review the tribe Stegaspidini at the generic level, based on comparative morphology. Keys for the identification of various stegaspidine taxa were outdated or nonexistent, and are here modernized. A summary of known distribution and biological data for the included taxa is provided, and for genera where sufficient material and information were available, species level revisions are presented. In all other cases, an updated species checklist is compiled following the generic description. The tribe will be reviewed in a series of three publications, with the present paper including a redescription of the tribe Stegaspidini, as well as treatments of the genera Bocydium, Lirania, and Smerdalea.

Amyot and Serville (1843a) recognized the group by the vernacular name "Bocydides" and Goding (1926e) called the same group "Acuminatini" (a nomen nudum). Haupt (1929c) established the subfamily Stegaspidinae (incorrectly spelled as Stegaspinae) to include four new tribes: Platycentrini, Stegaspidini (as Stegaspini), Stylocentrini, and Oedini. Many of the genera in these tribes had previously been placed in the membracid subfamily Centrotinae based on the exposed scutellum-Metcalf and Wade's (1965a) catalog listed Haupt's Oedini, Lycoderini, and Stegaspidini (as Stegaspini) as tribes of Centrotinae. Hamilton (1971b) moved seven "stegaspidine" genera (including Bocydium, Flexocentrus, Smerdalea, and Stylocentrus) to the family Aetalionidae under the subfamily "Stylocentrinae," but referred Stegaspis to the Membracinae (Membracidae).

Deitz (1975a) redefined the subfamily Stegaspidinae (as Stegaspinae), including the nominotypical tribe Stegaspidini (as Stegaspini, with the synonyms Stylocentrini Haupt 1929c, Stylocentrinae Haupt 1929c [sensu Hamilton 1971b], Oedini Haupt 1929c, Lycoderini Metcalf and Wade 1965a, and Bocydides Amyot and Serville 1843a). Based on certain wing features, Shcherbakov (1981a, b, 1982a, b) included Stylocentrus (in Stylocentrini), Bocydium, and Stegaspis in Aetalionidae. Deitz (1983b) emended the spelling of the subfamily and its nominotypical tribe to Stegaspidinae and Stegaspidini, respectively.

Selected stegaspidine genera have been included in various phylogenetic analyses of the Membracidae and related families. Strümpel (1972a) proposed a phylogeny of the Membracidae based primarily on pronotal structure, concluding that members of Stegaspidini arose from within the Centrotinae. Sakakibara's (1979) unpublished cladistic analysis of the Membracidae found that Smerdalea formed a clade with Stylocentrus, in Stegaspidini, rather than in Microcentrini where it had been placed. Finally, a recent phylogenetic analysis of the Membracoidea suggested that Stegaspidinae, consisting of the sister groups Microcentrini (sensu Deitz 1975a) and Stegaspidini (*sensu* Deitz 1975a, less *Euwalkeria* Goding), is a basal lineage of the family Membracidae (Deitz and Dietrich 1993a, Dietrich and Deitz 1993a); those works did not attempt to resolve relationships within the Stegaspidinae.

Metcalf and Wade's (1965a) catalog should be consulted for other references to the literature on members of Stegaspidini prior to 1956. Citations of membracid literature used in this work conform to the use of letter designations to indicate chronology of publication within a single year, initiated in Metcalf and Wade (1963a), and continued by later workers (Deitz and Kopp 1987a, Deitz 1989a, McKamey 1998a).

Deitz (1975a) distinguished Stegaspidini from related tribes based on diagnostic characters of the forewing (venation simple, not reticulate, with one m-cu crossvein), the metathoracic leg (femur lacking longitudinal row of cucullate setae; tibia triquetrous or foliaceous, lacking cucullate setae in row I. rows I and III, or rows I, II, and III), and the abdominal terga (lacking middorsal tuberosities). The definition of the tribe is here modified; as detailed below, the tribe Stegaspidini is now defined by the following combination of characters: forewing lacking reticulate venation, with one r-m and one m-cu crossvein, and vein R_{2+3} fused basally with R₁; metathoracic femur lacking cucullate setae; and male lateral plates are free and lacking posteroapical hooks or fused to the pygofer.

MATERIALS AND METHODS

Stegaspidine treehopper specimens were obtained through requests to New World and European collections and by a note in the *Tymbal*, an Auchenorrhyncha newsletter (Cryan and Bartlett 1994a). An endeavor was made to locate and examine the type species of all included genera, as well as the type material for many of the included species. The only genus not examined during this work was *Lirania*, for which descriptions and illustrations are based on those by Deitz (1975a). The following codens are used in this work to refer to the collections in which relevant specimens are located or have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†).

- AMNH: American Museum of Natural History, New York, New York, USA.
- BMNH: Department of Entomology, The Natural History Museum, London, United Kingdom.
- BPBM: Department of Entomology, Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
- CISC: Essig Museum of Entomology (California Insect Survey Collection), University of California, Berkeley, California, USA.
- CNCI: Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Research Branch, Ottawa, Ontario, Canada.
- GMPC[†]: Gérard Moragues Personal Collection, Marseille, France.
- IZAV: Instituto de Zoologiá Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.
- MNHN: National Collection of Insects, Muséum National d'Histoire Naturelle, Paris, France.
- MZLU: Museum of Zoology, Lund University, Helgonavägen, Lund, Sweden.
- NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.
- SEMC: Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA.
- SHMC[†]: S. H. McKamey Collection, currently at the United States Department of Agriculture, Agri-

cultural Research Service, Systematic Entomology Laboratory, % National Museum of Natural History, MRC-168, Washington, D.C., USA.

- TKWC[†]: T. K. Wood Collection, currently at the Department of Entomology and Applied Ecology, University of Delaware, Newark, Delaware, USA.
- USNM: Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.
- ZMUH: Zoologisches Institut und Zoologisches Museum, Universität von Hamburg, Hamburg, Germany.

Observations and illustrations were made using a Leitz[®] stereoscopic microscope (at 8 to $144 \times$ magnification) with an attached camera lucida. Measurements were taken with an ocular micrometer at $8 \times$ magnification. Genitalia dissections were prepared as described by Deitz (1975a); non-type specimens dissected during this work bear labels indicating "Cryan Research" numbers. Genitalia, and occasionally legs, were immobilized for illustration by imbedding part of the structure in a drop of boric acid ointment in glycerine. After examination and illustration, the dissected structures were placed inside the abdomen, which was then deposited in a microvial (either glass with a cork stopper or polypropylene with a rubber stopper) containing a small amount of glycerine for preservation. The vials were then pinned with their appropriate specimens.

A Philips 505T Scanning Electron Microscope was used to examine the pronota of selected stegaspidine species. The tree-hoppers so examined are pinned non-type and type specimens. Due to the scientific value and rarity of many of these specimens, they were scanned without the usual metal coating, using custom made specimen mounts (stubs) to accommodate the insect

pin. Electron microscopic examination without metal coating on the specimens necessitated the use of low voltage settings (\approx 5 kv) to reduce charging effects.

New species are described by the first author; all type specimens designated in this work are conspicuously labeled with colored labels (white with red outline for holotypes and white with blue outline for paratypes). Institutions where type specimens are deposited are listed in the relevant "Material examined" sections, along with quotations of label information. Where particular labels are quoted, the information from each label is enclosed in quotation marks, and individual lines within a label are separated by a virgule (/).

Distribution records are presented in two ways. In cases where only a generic review is given, all countries in which species of that genus have been found are listed under the heading "Range." For cases where species are treated individually, a separate "Distribution" section lists the countries where that species has been found. Following each distribution record is either a coden or a superscript number. Codens refer to a collection that includes specimens validating that record (only one collection is listed in most cases, although multiple collections may have specimens validating the distribution record). Superscript numbers document records from: 1Metcalf and Wade (1965a), not confirmed in this work and should be used with caution, as some may be based on misidentified species; and ²Cryan and Deitz (1995a), codens not included here to avoid redundancy. Unverified distribution records from Metcalf and Wade (1965a) should be used with caution. as some may be based on misidentified specimens.

Following the description of each genus and species treated in this work are brief remarks concerning items of interest peculiar to that taxon. Included in these sections are any references to host-plant identities, biology and life-history notes, collection and habitat information, and hypotheses concerning the relationships of the taxa to other groups.

MORPHOLOGICAL CHARACTERS

The taxonomically important morphology for the subfamily Stegaspidinae, including Stegaspidini, is illustrated in Figs. 1–8. The terminology used in this work follows recent usage for Membracidae (Deitz 1975a—general morphology; McKamey and Deitz 1991c—morphology of the pronotum; Capener 1962a—supraocular callosities, centro-ocular line).

Taxonomically useful features of the stegaspidine head (Fig. 1) include the relative size of the dorsal projections, location of the ocelli relative to the centro-ocular line, the nature (size and shape) of the foliate lobes, and the shape of the frontoclypeus (uni- or trilobed). In addition, many species of Stegaspidini have the compound eyes and ocelli sessile, not stalked (Figs. 19–20), whereas the compound eyes and ocelli of some species are stalked (Fig. 23; Deitz 1975a fig. 40C).

The thorax, with the legs and wings, holds many characters informative at a variety of taxonomic levels. These include the structure of the pronotum (Fig. 2; shape of the metopidial region suprahumeral horns, posterior process, and humeral angles), nature of the scutellum (Figs. 2, 13, 20; apex emarginate or acuminate), shape of the tibiae (Fig. 3, not foliaceous; Deitz 1975a: fig 39d, foliaceous), chaetotaxy of the metathoracic leg (Fig. 3; presence or absence of cucullate setae on the femur and in the three enlarged setal rows of the tibia), and forewing structure and venation (Fig. 4; extent of wing that is coriaceous, number and location of crossveins, and branching patterns of vein R). Other thoracic features include the surface sculpturing of the pronotum (Figs. 28-30; shape of ultrastructural pits and associated setae) and the presence of supraocular callosities.

Some descriptions include mention of the metopidium (the pronotal region dorsad of the anterior 'face' of the head). In some



Figs. 1–8. Diagrammatic Morphology of Stegaspidini. 1, Head, anterior aspect (face). 2, Head, pronotum, and scutellum, anterolateral aspect. 3, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 4, Right forewing. 5, Female second valvulae, lateral aspect. 6, Male pygofer and posterior lobe (fused lateral plate). left lateral aspect. 7, Male left lateral plate (free, not fused), lateral aspect. 8, Male aedeagus and left style, lateral aspect. Abbreviations: $A_{\#}$ = anal veins; aa, anterior arm; ac = anteclypeus: ae aedeagus; ah, apical hook; an = antenna; ce, compound eye; Cu_1 = cubital vein; di = distal setal row; do = dorsal setal row; dp = dorsal projection; ds = dorsal serrations; fc = frontoclypeus; fe = femur; fl = foliate lobe; ha = humeral angle; lo = lorum; lp = lateral plate; $M_{\#}$ = medial vein(s); mc = median carina; me = metopidium; oc = ocellus; pa = posterior arm; pc = frontoclypeus; pl = posterolateral process; pp = posterior pronotal process; py = pygofer; $R_{\#}$ = radial vein(s); sc = scutellum; sh = suprahumeral horn; so = supraocular callosity; st = subapical teeth; sy = style; ve = vertex; 1, II, III = enlarged setal rows.

species, the metopidium is not elevated (Fig. 24), sloping smoothly to the posterior pronotal process; in other species (Figs. 11, 13) the metopidium is elevated, often bearing the suprahumeral horns and the posterior pronotal process high above the body of the insect. We consider any pronotal extensions located above the humeral angles to be suprahumeral horns. Thus, the stalked bulbs of Bocydium spp. (Figs. 9, 11, 13), the unbranched triquetrous processes of Lycoderes spp. (Deitz 1975a: fig. 40T), and the sometimes trifurcating horns of Smerdalea spp. (Fig. 24) are homologous. The location and structure of suprahumeral horns vary greatly within the tribe Stegaspidini, and even within some genera; nevertheless, the nature of these pronotal extensions usually provides excellent taxonomic features at the specific and generic levels.

Abdominal characters center on the male and female genitalia. Characters of the female genitalia include shape and degree of serration of the second valvulae (Fig. 5). Valuable features of the male genitalia include the degree of fusion and structure of the lateral plates (fused to pygofer completely or basally [Fig. 6], or entirely free [Fig. 7]), structure of the styles (Fig. 8; width and shape of the apical hook), and structure of the aedeagus (Fig. 8; width, shape, and surface features of anterior face of posterior arm). All known stegaspidine nymphs have setose abdominal lamellae and emarginate wingpads (Figs. 10, 22).

Measurements recorded include the total length of the body with wings in repose (from head to apex of forewings), length of the pronotum, width between the humeral angles, length of the forewings, and the maximum width of the centro-ocular line (maximum width of head across eyes).

TRIBE STEGASPIDINI HAUPT 1929C

- Bocydides Amyot and Serville 1843a: 551 [a vernacular name].
- Acuminatini Goding 1926e: 297 [Nomen nudum]

Stegaspini Haupt 1929c: 228. Emended to Stegaspidini Haupt 1929c: Deitz 1983b: 856.

Stylocentrini Haupt 1929c: 228.

Stylocentrinae Haupt 1929c: 228.

Oedini Haupt 1929c: 228.

Lycoderini Metcalf and Wade 1965a: 45.

Diagnosis.—Species of Stegaspidini have the forewing with 1 r-m and 1 m-cu (usually basad of the fork of vein M) crossvein and vein R_{2+3} fused basally with R_1 ; the δ lateral plates either free (without posteroapical hooks) or basally fused to the pygofer.

Adult.—Dimensions (mm): Total length 3.2-13.8. Structure: Head: Compound eyes and ocelli stalked (Fig. 12) or not (Fig. 19); ocelli above centro-ocular line (exception: ocelli of Smerdalea on or below centro-ocular line); dorsal projections generally small (with some exceptions). Thorax: Pronotum: Middorsal crest present, extending over partial or entire length of pronotum; posterior process extending over scutellum (dorsally concealing scutellum or not; scutellum usually not concealed laterally except in at least one species-Lycoderes phasianus Fowler). Pronotal surface sculpturing (Figs. 28-30): Punctate; generally, one seta associated with each pit; surface smooth or tuberculate. Legs: Metathoracic femur usually lacking cucullate setae (at least, dorsal band of cucullate setae absent); metathoracic tibiae foliaceous (Deitz 1975a: fig. 39D) or not (Fig. 14), with cucullate setae in rows II and (in some species) III. Forewing (Fig. 4): 1 r-m and 1 m-cu crossvein present. Genitalia: 9 2nd valvulae slightly broadened or of uniform width, with dorsal serrations on distal region; ∂ lateral plate either free, without hook, or basally fused to pygofer.

Late-instar nymph.—Body slightly flattened dorsoventrally; pronotum with or without carinae or horns, often produced into a laterally compressed hump; all tibiae foliaceous; abdominal segments 4–8 with platelike lateral lamellae. Range.—Argentina to Mexico, including Trinidad.

Remarks.—As stated by Deitz (1975a), the reduction in forewing venation and in numbers of metathoracic tibial rows of cucullate setae in Stegaspidini indicate that this group is derived in more features than is its sister tribe, Microcentrini. In addition, the elaborate pronota of most Stegaspidini suggest more specialized forms of crypsis than seen in most Microcentrini (Cryan and Deitz, in press). The conspicuous, chalazaefringed abdominal lamellae of Stegaspidini nymphs (also evident in Microcentrini) are similar to those of the nymphs of Nessorhininae, Procyrtini (Darninae), and most Centrotinae (S. H. McKamey, personal communication).

Little is known about the biology and life histories of these treehoppers. Members of Stegaspidini are recorded from the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae. Microbial endosymbionts have been recorded from *Bocydium globulare, Lycoderes galeritus,* and *L. mitratus* (Müller 1949a, Buchner 1953a). Haviland (1925a) observed adults of *Flexocentrus felinus* [as *Centruchoides felinus*] and *Stegaspis fronditia* [as *S. galeata*] with ant attendants. Additional information is recorded for some species (see individual descriptions).

Key to the Genera of Adult Stegaspidini

1.	Tibiae not foliaceous; hind tibia with cucullate
	setae in enlarged setal rows 1, II, and/or III en-
	larged setal rows 3
_	All tibiae foliaceous; hind tibia with cucullate
	setae in enlarged setal row II only, or absent
	2
2.	Suprahumeral horns absent (Fig. 20); hind tibia
	without cucullate setae Lirania Stål
_	Suprahumeral horns present, pyramiform
	(Deitz 1975a: fig. 40Q); hind tibia with cucul-
	late setae in row 11 Flexocentrus Goding
3.	Metopidium gibbous, not elevated 5
_	Metopidium elevated, usually laterally com-
	pressed 4
4.	Cranial foliate lobes not extending over fron-
	toclypeus (Fig. 1); suprahumeral horns present,
	though sometimes very small at apex of elon-

gate dorsal metopidium (Deitz 1975a: fig. 40T); posterior pronotal process variable

- Cranial foliate lobes extending over frontoclypeus (Deitz 1975a: fig. 40B), suprahumeral horns absent (Deitz 1975a: fig. 40U); posterior pronotal process laterally compressed, leaflike (Deitz 1975a: fig. 40U) Stegaspis Germar
- Forewing with vein A₁ partially confluent with claval suture and distal m-cu crossvein distad of fork of vein M (Fig. 26) . . Smerdalea Fowler

- Head with distinct dorsal projections (Deitz 1975a; figs. 40E–F); ♂ lateral plates fused to
- - Posterior pronotal process simple, spinelike;
- suprahumeral horns long, branched, bearing inflated bulbs (Fig. 11) *Bocydium* Latreille
- Suprahumeral horns unbranched (Deitz 1975a: fig. 400); hind tibia with cucullate setae in row II and in distal ¹/₃ of row III (row 1 with 1–3 cucullate setae distally) Stylocentrus Stål
- Suprahumeral horns branched (Deitz 1975a: fig. 40P); hind tibia with cucullate setae in rows II and III or II only . . Umbelligerus Deitz

Genus Bocydium Latreille, 1829a

- *Bocydium* Latreille 1829a: 219. Type species: *Centrotus globularis* Fabricius 1803a by subsequent designation of Blanchard 1849c: 614.
- *Sphaeronotus* de Laporte 1832b: 229. Type species: *Centrotus globularis* Fabricius 1803a, by original designation.

Diagnosis.—Species of *Bocydium* are easily recognized by the inflated bulbs on the suprahumeral horns.

Adult.—*Dimensious* (mm): Total length 4.6–7.5. *Structure: Head* (Fig. 12): Dorsal projections small or absent; compound eyes and ocelli not stalked; frontoclypeus weakly trilobed. *Thorax: Pronotum* (Figs. 9, 11, 13): Slender suprahumeral horns (bearing inflated bulbs [lobes] of various sizes,



Figs. 9–10. *Bocydium* species. 9, *B. amischoglobian* (anomolous specimen), head, pronotum, and scutellum, anterolateral aspect. 10, *B. rufiglobum*, late-instar nymph, lateral aspect.

shapes, and numbers) and simple, spinelike posterior process arising from central pronotal stalk (elevated metopidium). *Pronotal surface sculpturing* (Fig. 28): Punctate, each pit associated with 1 long, narrow seta; surface finely tuberculate between pits. *Legs* (Fig. 14): Tibiae simple, not foliaceous; metathoracic tibia with cucullate setae in rows II and III only. *Forewing* (Fig. 15): 1 r-m and 1 m-cu crossvein present; r-m crossvein basad of branch of vein M. *Genitalia*: \Im 2nd valvulae (Fig. 16) slightly broadened at midlength, with dorsal serrations on distal half; \eth lateral plate (Fig. 17) free, without posteroapical hook.

Late-instar nymph.—Known only for *B.* rufiglobum Fairmaire (Fig. 10) and *B. cubitale* Richter (1955a: fig. 6B): pronotum laterally flattened, metopidium vertically produced into median horn with darker internal structure visible through integument; tibiae foliaceous, fringed with setae; lateral lamellae, present on abdominal segments 4– 8, fringed with setae.

Range.—Paraguay¹; Bolivia [AMNH]; Brazil [NCSU]; Peru [NCSU]; Ecuador [USNM]; Colombia [ZMUH]; French Guiana [CNC1]; Suriname [ZMUH]; Guyana [NCSU]; Venezuela [IZAV]; Costa Rica [TKWC]; Trinidad [USNM].

Material examined.—16 specimens from AMNH (including holotype of *Bocydium bullifera* Goding [φ] with labels: "Bolivien," "Matausch Coll./Ac. 4883," "A. Mus. Nat. Hist./Dept. Invert. Zool./No.," "Bocydium/S. Bol.," "Deitz Research/72-81e φ ," "Bocydium/bulliferum/type Goding.," and "HOLOTYPE/BOCYDIUM/ BULLIFERA/Goding"); 29 from BMNH; 6 from BPBM; 1 from CISC; 8 from CNCI; 18 from IZAV; 5 from MZLU; 82 from NCSU; 1 from SEMC; 31 from SHMC; 11 from TKWC; 32 from USNM; 104 from ZMUH (including Cryan Research #93-353a φ).

Remarks.—Funkhouser (1951a) characterized *Bocydium* as "one of the most remarkable of all of the genera of the Membracidae and with structures as curious and

bizarre as those of any insect family surely from the signs which are displayed above their heads, these must be the pawnbrokers among insects." Members of this genus are usually small, dark insects with a delicate appearance. Although Poulton (in Buckton 1903b) advanced the possibility that the pronota mimic Neotropical seeds or small, spiny fruit, the actual function of the peculiar pronotal structures is unknown, as are the life histories of many of the species. Richter (1955a) reported B. astilatum and B. nigrofasciatum from an unidentified plant belonging to the Melastomataceae and B. cubitale from Pithocarphya poeppigiana (Asteraceae); Wood (1984a) reported B. globulare on Miconia sp. (Melastomataceae). McKamey (personal communication) collected Bocydium on Vismia sp. (Guttiferae); Haviland (1925a) reported that B. globulare usually occurs only a few feet above the ground, feeding on the undersides of leaves. Adults of this genus seem to be solitary, although multiple specimens have been taken from branches of the same tree (Wood 1984a).

Species of Bocydium are frequently illustrated as examples of strange treehoppers. Illustrations of Bocydium sp., prob. globulare, appear in publications by Vignon (1930a), Heikertinger (1954a), Seitz (1951a), and Suchantke (1983a). A photograph of Bocydium sp. (as "B. rufiglabrum" in the figure caption) was published by Parenti (1971a, 1972a), whereas Klausnitzer (1987a) published a picture of B. amischoglobum (as "B. rufiglobum" in the figure caption) and Boulard (1986a) published a photograph of B. globulare. Strümpel (1983a) published a scanning electron micrograph of the full body of B. globuliferum.

An unusual specimen of *B. amischoglobum* (from ZMUH, bearing label "Cryan Research #93-353a \Im ") is illustrated here (Fig. 9). The normal condition for this species (and all others in this genus) is for the posterior pronotal process to extend posteriorly. This aberrant individual has the posterior process extending dorso-anteriorly, much like a unicorn.

Sakakibara (1981c) published a partial revision of this genus; because of this recent work, the treatment of *Bocydium* here is limited to the following: the description of one new species of *Bocydium*; a taxonomic key, modified from Sakakibara (1981c) to include all *Bocydium* species (original descriptions of six species not examined in the present work did not give diagnoses sufficient for unqualified taxonomic separation; thus, those species are grouped as potential identities in the key, below); and a synonymic checklist of the species.

Bocydium duoglobum Cryan, new species (Figs. 11–18, 29)

Type locality.—Barbacoas, Nariño, Co-lombia.

Diagnosis.—*Bocydium duoglobum* has each suprahumeral horn with only a single, stalked bulb (Figs. 11, 13). The suprahumeral horns and the posterior pronotal process project obliquely upwards from a long, posteriorly curved stalk.

Adult.-Dimensions (mm): Total length , δ 4.6–4.8; width between humeral angles 1.4, δ 1.2–1.4; pronotal height 2.1, ♂ 1.9-2.9; wing length ♀ 4.1, ♂ 3.6-4.0; maximum width of head across eyes 1.4, & 1.3-1.4. Coloration: Head and thorax dark brown, nearly black, with or without pale wax patterns; abdomen and legs tan; wings hyaline with brown patches. Structure: Head: Face (Fig. 12) sparsely setose; with or without waxy secretions in defined patterns; eyes not stalked; ocelli on slightly raised tubercles; dorsal projections small, separated by distance equal to separation of ocelli; dorsal transverse ridge small; post-frontal sutures obscure; frontoclypeus produced ventrally. Thorax: Pronotum (Fig. 13): With short setae, except for suprahumeral horns and posterior process, which bear sparse, long setae; with or without waxy secretions in defined patterns; supraocular callosities obscure; humeral angles somewhat produced, but not acute; dorsal carina obscure; suprahumeral horns each with 2 branches: lateral branches simple, spinelike, and anterior branches each bearing a stalked bulb; posterior process simple, spinelike, of roughly equal length to lateral branches of suprahumeral horns; suprahumeral horns and posterior process arise from long, posteriorly curved pronotal stalk at approximately same point, then project obliquely upwards; internally, suprahumeral horns divided into 3 hollow tubes: a large center tube flanked by 2 smaller tubes (Fig. 29). Pronotal surface sculpturing (Fig. 29): Metopidium punctate, each pit associated with 1 long, narrow seta; pits on pronotal stalk often oblong, slitlike (rather than round); surface of suprahumeral horns and posterior pronotal process tuberculate. Scutellum (Fig. 13): Short; elevated anteriorly, then flattened to acuminate apex; darkly pigmented anteriorly, with distal area bright yellow. Legs (Fig. 14): Metathoracic femur with 2 or 3 dorsal cucullate setae apically; metathoracic tibia with cucullate setae only in setal rows II and III; row II with cucullate setae throughout, row III with cucullate setae in apical 1/3. Forewing (Fig. 15): Basal 1/3 thickened, punctate (except area between claval suture and vein Cu), obscuring vein A2; crossvein r-m₁ absent or an incomplete stub. Genita*lia:* \mathcal{Q} : 2nd valvulae (Fig. 16) abruptly broadened at about ²/₃ of their length, tapering to dorsally curved apex; dorsal ridge of broadened area without distinct serrations; δ : Lateral plates (Fig. 17) free, without apical hook; styles (Fig. 18) hooked apically (resembling the bill of a bird); aedeagus (Fig. 18) strongly U-shaped, tapering apically, anterior face of posterior arm not denticulate.

Late-instar nymph.—Unknown.

Distribution.—Colombia: Nariño [BMNH].

Material examined.—Holotype: [♂] [BMNH], with labels "COLOMBIA: Na-/



Figs. 11–18. *Bocydium duoglobum*, structures of the holotype (genitalia illustrated from the paratypes). 11, Full body, anterolateral aspect. 12, Head, anterior aspect (face). 13, Head, pronotum, and scutellum, anterolateral aspect. 14, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 15. Right forewing. 16, Female second valvulae, lateral aspect. 17, Male left lateral plate, lateral aspect. 18. Male aedeagus and left style, lateral aspect.

rino, Barbacoas/5.I.1975/M. Cooper/B.M. 1975-33" and "HOLOTYPE δ /*Bocydium*/ *duoglobum*/J. R. Cryan." Paratype: [\mathfrak{Q} , dissected, with posterior pronotal process broken; BMNH], with labels "COLOMBIA:/ Narino, Barba-/coas.19-21.vii.1974/M. Cooper/B.M. 1974-548" and "PARATYPE \mathfrak{Q} /*Bocydium*/*duoglobum*/J. R. Cryan." Other specimens: 2 δ (1 with missing head and pronotum, and 1 [dissected] with wings missing) from BMNH (including Cryan Research #94-253a δ).

Remarks.—*Bocydium duoglobum* resembles *B. germarii* Guérin-Méneville in that each suprahumeral horn bears only one bulb, but *B. duoglobum* differs in having the bulbs stalked. Also, the lateral branches of the suprahumeral horns are simple (those of *B. germarii* bear reduced bulbs), and the suprahumeral horns and the posterior pronotal process rise obliquely from the pronotal stalk (in *B. germarii*, they extend away from the pronotal stalk at nearly 90° angles). *Bocydium duoglobum* is much darker than *B. germarii*.

The specific name is a combination of the Latin terms "duo" (meaning "two") and "globum" (from "globus," meaning "ball or sphere"), referring to the structure of the suprahumeral horns.

Key to Species of Adult *Bocydium* (Modified from Sakakibara 1981c)

1.	Lateral branches of suprahumeral horns each with, at most, a single globe 2
_	Lateral branches of suprahumeral horns each with two globes <i>B. sexvesicatum</i> Sakakibara
2.	Lateral globes smaller than the anterior globes, or lacking
	Lateral globes equal to or larger than the an-
3.	Anterior globes normal, lateral globes re-
-	Both anterior and lateral globes reduced or
	B. germarii Guérin-Méneville
4.	Lateral globes fusiform
_	Lateral globes lacking entirely (Fig. 11) B. duoglobum Cryan, new species
5.	Anterior globes petiolate 6
-	Anterior globes not petiolate (Fig. 9) B. amischoglobum Sakakibara, B. astilatum Richter, B. cubitale Richter, or B. bulliferum Goding
6.	Lateral globes noticeably larger than anterior
_	Lateral globes subequal to anterior globes 8
7.	Lateral globes ellipsoidal in outline B. rufiglobum Fairmaire
_	Lateral globes more or less triangular in out- line <i>B</i> anisobullatum Sakakibara
8.	Maximum distance between lateral globes smaller than double the width between hu- meral angles
-	Maximum distance between lateral globes larger than double the width between humeral
9.	angles <i>B. globulare</i> (Fabricius) Lateral spines longer than the diameter of the
	Lateral spines shorter than the diameter of the lateral globes; coloration generally chestnut-
	B. racemiferum Sakakibara and B. nigrofascia- tum Richter

10.	\mathcal{Q} subgenital plate normal; \mathcal{J} subgenital plate
	also normal, but with long hairs
	B. globuliferum (Pallas)
	\mathfrak{P} subgenital plate bilobed; \mathfrak{F} subgenital plate
	substantially lengthened, outwardly curved,
	and with short hairs
	B. tintinnabuliferum Lesson

SPECIES CHECKLIST OF BOCYDIUM

amischoglobum Sakakibara Bocydium amischoglobum Sakakibara 1981c: 825. anisobullatum Sakakibara Bocydium anisobullatum Sakakibara 1981c: 825. astilatum Richter Bocydium astilatum Richter 1955a: 278. bulliferum Goding Bocydium bullifera Goding 1930b: 4. cubitale Richter Bocydium cubitale Richter 1955a: 280. duoglobum Cryan, new species germarii Guérin-Méneville Bocydium germarii Guérin-Méneville 1844a: 366. Bocydium germari: Fairemaire 1846b: 509. Unjustified emendation. globulare (Fabricius) Centrotus globularis Fabricius 1803a: 16. globularis: Membracis Latreille 1818c: 123. Bocydium globulare: Latreille 1829a: 219. Sphaeronotus globularis: de Laporte 1832b: 229. globuliferum (Pallas) Cicada globulifera Pallas 1766a: 187. Cicada globulare [sic]: Blanchard 1840a: 184. Bocydium globuliferum: Walker 1851a: 601. nigrofasciatum Richter Bocydium nigrofasciatum Richter 1955a: 273. racemiferum Sakakibara Bocydium racemiferum Sakakibara 1981c: 827.

- rufiglobum Fairmaire
- *Bocydium rufiglobum* Fairmaire 1846b: 508.
- sexvesicatum Sakakibara
 - *Bocydium sexvesicatum* Sakakibara 1981c: 823.
- sphaerulatum Sakakibara
 - *Bocydium sphaerulatum* Sakakibara 1981c: 826.
- tintinnabuliferum Lesson
 - Bocydium tintinnabuliferum Lesson 1832a: [1].
 - *Bocydium glomeriferum* Germar 1835a: 260.
 - Bocydium globiferum [sic] Blanchard 1840a: 184.
 - Lycoderes tintinnabuliferum: Heymons 1926a: [I].
 - Bocydium tintinnabuliferum: Funkhouser 1927f: 350.

Genus Lirania Stål 1862e

Lirania Stål 1862e: 36. Type species: *Lirania bituberculata* Stål 1862e: 36, by original designation and monotypy.

Diagnosis.—*Lirania* is unique among Stegaspidinae in entirely lacking cucullate setal rows on the metathoracic tibiae.

Adult.—*Structure: Head:* Dorsal projections distinct. *Thorax: Pronotum:* Suprahumeral horns absent; posterior pronotal process long, unbranched. *Scutellum:* Apex emarginate. *Legs:* Pro- and mesothoracic tibiae foliaceous; metathoracic leg lacking cucullate setae. *Forewing:* Vein R_{2+3} fused basally with R_1 ; r-m crossvein distad of fork of vein M.

Range.—Brazil.

Remarks.—The etymology of the generic name was not described by Stål (1862e), although it may be based, in part, on the Latin "*lira*," meaning "a ridge."

Lirania bituberculata Stål 1862e (Figs. 19–21)

Lirania bituberculata Stål 1862e: 36.

Type locality.—Rio de Janeiro, Brazil. Diagnosis.—*Lirania bituberculata* has a simple posterior pronotal process but lacks suprahumeral horns and cucullate setal rows on all the metathoracic tibiae.

Adult 9.—*Structure: Head* (Fig. 19): Dorsal projections distinct; eyes neither stalked nor prominent; frontoclypeus trilobed. Thorax: Pronotum (Fig. 20): Middorsal carina present; suprahumeral horns absent; posterior pronotal process expanded midway, tapering to acuminate apex. Scutellum (Fig. 20): Flat for entire length; apex emarginate. Legs: Pro- and mesothoracic tibiae foliaceous; metathoracic femur and tibia lacking cucullate setae in all rows. Forewing (Fig. 21): Apical margin rounded; vein R_{2+3} fused basally with R_1 ; 1 r-m and 1 m-cu crossvein present (r-m crossvein distad of fork of vein M). Genitalia: Not examined. d: Unknown.

Late-instar nymph.—Unknown. Distribution.—Brazil: São Paulo¹.

Material examined.-None.

Remarks.—Although no specimens of *Lirania bituberculata* were examined in this work, Deitz (1975a) examined the lectotype and illustrated the forewing, head, and pronotum of this species (Deitz 1975a: figs. 38F, 40F, and 40R, respectively; redrawn here as Figs. 19–21). Our concept of *L. bituberculata* is based on these figures and the original description (Stål 1862e).

The specific name is a combination of the Latin terms "bi" (meaning "two") and "*tuberculata*" (meaning "tuberculate"), possibly referring to the prominent dorsal projections of the head.

Genus *Smerdalea* Fowler 1896e, new tribal placement

Smerdalea Fowler 1896e: 162. Type species: *Smerdalea horrescens* Fowler 1896e: 163, by monotypy.

Diagnosis.—The genus *Smerdalea* differs from other genera of Stegaspidini by having an elongate posterior pronotal process that terminates in a strongly dilated node with multiple spines. The forewing



Figs. 19–21. *Lirania bituberculata*, structures of the lectotype. 19, Head, anterior aspect (face). 20, Head, pronotum, and scutellum, anterolateral aspect. 21, Right forewing.

vein A₁ is partially confluent with the claval suture, and one r-m crossvein is present.

Adult.-Dimensions (mm): Total length 7.8-11.0. Structure: Head: Compound eyes elongate transversely, stalked or nearly so; ocelli on raised tubercles; dorsal projections distinct. Thorax: Pronotum (Fig. 24): Pronotum with humeral angles nearly acute; metopidium with distinct supraocular callosities; suprahumeral horns prominent; posterior pronotal process elongate, terminating with dilated node bearing multiple spines. Pronotal surface sculpturing (Fig. 30): Surface scabrous and punctate, each pit with one long, associated seta. Scutellum (Fig. 24): Elongate, usually dorsally produced at base, apex acuminate or emarginate. Legs (Fig. 25): Metathoracic femur with dorsal row of cucullate setae present; metathoracic tibia with 3 rows of enlarged, cucullate setae; metathoracic tarsomere I

with apical cucullate seta. *Forewing* (Fig. 26): Coriaceous basally, with 1 r-m crossvein and vein A₁ partially confluent with claval suture. *Genitalia*: 9: 2nd valvulae (Fig. 27) broadened abruptly at or past midlength, tapering distally, serrate dorsally; δ (Cryan and Deitz 1995a: fig. 6): styles hooked apically; aedeagus with anterior face of posterior arm denticulate preapically.

Range.—Peru²; Ecuador [USNM]; French Guiana [GMPC]; Panama²; Costa Rica [CNCI]; Guatemala²; Mexico [CNCI].

Material examined.—In addition to the specimens examined by Cryan and Deitz (1995a): $2 \$ *S. horrescens* [CNCI].

Remarks.—Cryan and Deitz (1995a) recently revised the genus *Smerdalea*. Included in the present treatment of this genus is a description of one new species, a description of the previously unknown nymph of



Fig. 22. Smerdalea elevata, late-instar nymph, anterolateral aspect.

S. elevata Cryan, and an updated key and a checklist to the species of *Smerdalea*.

KEY TO SPECIES OF SMERDALEA

1.	Apex of scutellum emarginate 2
_	Apex of scutellum acuminate
2.	Pronotum with trifurcate suprahumeral horns
	(Fig. 24); basal node of posterior pronotal pro-
	cess with distinct tooth (Fig. 24)
	S. imminens Cryan, new species
_	Pronotum with suprahumeral horns culminat-
	ing in a single process (Cryan and Deitz 1995a:
	fig. 9); basal node of posterior pronotal process
	lacking tooth (Cryan and Deitz 1995a: fig. 9)
	S. circumflexa Cryan
3.	Posterior pronotal process elevated high above
	scutellum (Cryan and Deitz 1995a: fig. 16);
	scutellum not produced subapically (Cryan and
	Deitz 1995a: fig. 16) S. elevata Cryan
	Posterior pronotal process touching or nearly
	touching scutellum (Cryan and Deitz 1995a:
	fig. 2); scutellum produced subapically (Cryan
	and Deitz 1995a: fig. 2) S. horrescens Fowler

Smerdalea elevata Cryan (Fig. 22)

Late-instar nymph (Fig. 22).—Body dorsoventrally compressed; pronotum with stout precursors of suprahumeral horns and posterior process, in form resembling the adult but not elevated; mesonotum with lateral, comb-like row of bristles at base of each wing pad and paired dorsal chalazae; legs thin, not foliaceous; abdominal segments 4–8 with setose lateral lamellae and 1 stout seta on either side of dorsal midline; anal tube (abdominal segment 9) thin, slightly longer than other abdominal segments in dorsal view, with paired dorsal rows of stout setae at base.

Material examined.—1 nymph [USNM].

Remarks.-Smerdalea elevata was described from three females, all collected from the same forest plot (in the Río Tambopata Reserved Zone, Madre de Dios, Peru) by the Smithsonian Institution's Canopy Fogging Project. After the description was published, a single nymph was found in the same sample that yielded the adult type specimens. The posterior pronotal process of the nymph leaves no doubt as to its genus. Despite the fact that this nymph cannot be directly associated with the S. elevata adults, no other Smerdalea species are recorded from this locality. Thus, this specimen is thought to be the late-instar nymph of S. elevata.

Smerdalea imminens Cryan, new species (Figs. 23–27)

Type locality.—Reserva Ethnica Waorani, Napo, Ecuador.

Diagnosis.—*Smerdalea imminens* has an emarginate scutellum and trifurcate suprahumeral horns.

Adult \bigcirc .—*Dimensions* (mm): Total length 8.9–9.2; width between humeral angles 3.5–3.7; pronotal length 5.3–6.0; wing length 7.8–7.9; maximum width of head



Figs. 23–27. *Smerdalea imminens*, structures of the holotype. 23, Head, anterior aspect (face). 24, Head, pronotum, and scutellum, anterolateral aspect. 25, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 26, Right forewing. 27, Female second valvulae, lateral aspect.

across eyes 3.4–3.7. *Coloration:* Head and thorax mottled light and dark brown; apical node of posterior pronotal process dark brown with tan terminal spines tipped with black; legs light brown with dark brown transverse bands; forewings hyaline with dark brown maculae. *Structure: Head:* Face (Fig. 23) with fine pubescence; eyes stalked, transversely elongate; ocelli located just below centro-ocular line on low tubercles; dorsal projections distinct, separated by distance just greater than separation between ocelli, and bordering dorsal transverse ridge. *Thorax: Pronotum* (Fig. 24): Sparsely covered with fine, pale setae; metopidial sulcus depression with distinct supraocular callosities; humeral angles produced, nearly acute; suprahumeral horns smoothly edged (not serrate), rising obliquely away from body (in anterior aspect), trifurcate at about ½ length with central process largest; dorsal transverse ridge evident from each central process to base of suprahumeral horn; posterior pronotal process arched, with basal and apical nodes; basal node unadorned; apical node laterally

compressed, with one stout dorsal spine and three posterior spines of subequal length; apical node rests in scutellar emargination. Scutellum (Fig. 24): Elongate, elevated anteriorly, then flattened; apex emarginate and slightly raised to meet apical node of posterior pronotal process. Legs (Fig. 25): Metathoracic femur with dorsal row of 7-12 cucullate setae: metathoracic tibia with enlarged setal rows I, II, and III distinct, each bearing cucultate setae (22-26, 25-29, and 30-34, respectively); area between setal rows I and II slightly sulcate. Forewing (Fig. 26): Basal ¹/₃ coriaceous (except area between claval suture and Cu). Genitalia: 2nd valvulae (Fig. 27) abruptly broadened at about ²/₃ of its length, remaining broadened to apex; dorsal ridge of broadened apical $\frac{1}{3}$ with distinct servations. δ : Unknown.

Late-instar nymph.—Unknown.

Distribution.—Ecuador [USNM]; French Guiana [GMPC].

Material examined.—Holotype [9, dissected] [USNM] with labels: "MEMB 172/ LOT #870," "ECUADOR: NAPO Res. Ethnica/Waorani, 1 km S. Onkone Gare/ Camp, Trans.Ent. 6 Oct. 1994/220 m 00°39'10" S 076°26'W/T. L. Erwin et. al," "Insecticidal fogging of mostly bare/green leaves, some with covering/of lichenous or bryophytic plants in/terre firme forest At trans 9,/Sta. 1 Project MAXUS Lot870." and "HOLOTYPE/Smerdalea/imminens/J. R. Cryan." Paratype [9] [GMPC] deposited in MNHN, with labels: "GUYANE (Régina)/Montagne de Kaw/PK36 22.IX.93/G. MORAGUES," "piège lumineux," and "PARATYPE/Smerdalea/imminens/J. R. Crvan."

Remarks.—*Smerdalea imminens* is closely related to *S. circumflexa* Cryan, as evidenced by the emargination of the scutellum. These species differ principally in the nature of the suprahumeral horns (*S. circumflexa* has unbranched suprahumeral horns) and in the shape of the female ovipositor (the 2nd valvulae of *S. imminens* and *S. circumflexa* have the same general shape, although the 2nd valvulae of the former is narrower).

The specific name is from the Latin "immineo" (to threaten), referring to the threatening, dangerous appearance of this species.

SPECIES CHECKLIST OF SMERDALEA

circumflexa Cryan

Smerdalea circumflexa Cryan, in Cryan and Deitz 1995a: 9.

elevata Cryan

Smerdalea elevata Cryan, in Cryan and Deitz 1995a: 10.

horrescens Fowler

Smerdalea horrescens Fowler 1896e: 163.

imminens Cryan, new species

Smerdalea imminens Cryan, new species

SUMMARY

Recent taxonomic changes in the tribe Stegaspidini are summarized in Table 1. Currently, two stegaspidine genera are monotypic: *Flexocentrus* (*F. felinus*, for which both sexes are known) and *Lirania* (*L. bituberculata*, known only from a female specimen). Immature stages are unknown for all species of the genera *Lirania*, *Oeda*, *Stylocentrus*, and *Umbelligerus*.

Biogeographically, the tribe Stegaspidini is most diverse in the mid-latitudes of South America. The distribution of the nine stegaspidine genera is as follows: Mexico (2 genera), Guatemala (2), Honduras (2), Nicaragua (1), Costa Rica (6), Panama (5), Colombia (5), Trinidad (3), Venezuela (7), Guyana (7), Suriname (5), French Guiana (7), Ecuador (7), Peru (7), Brazil (8), Bolivia (5), Paraguay (2), and Argentina (2).

Information regarding stegaspidine host plants needs to be increased. Reliable host records are available for only a few species in the genera *Bocydium*, *Flexocentrus*, *Lycoderes*, *Oeda*, and *Stylocentrus*. To date, records for these genera are from the plant families Asteraceae, Guttiferae, Melastomataceae, Moraceae, and Rubiaceae. In addition,



Figs. 28–30. Pronotal metopidium surface sculpturing of Stegaspidini. 28, *Bocydium globulare*. 29, *B. duo-globum.* 30, *Smerdalea elevata*.

questions regarding voltinism, degree of presociality, and forces behind the development and evolution of the often-bizarre pronotal shapes of these insects remain unanswered.

Stegaspidini is the nominate tribe of Stegaspidinae, one of the more plesiomorphic membracid subfamilies (Dietrich and Deitz 1993a). Certain morphological characters appear more derived in Stegaspidini than in its sister tribe, Microcentrini; the evolutionary relationships among the tribes and genera of Stegaspidinae will be explored in a phylogenetic analysis of the subfamily (Cryan and Deitz, in preparation).

Deitz 1975a ¹	Cryan and Deitz (present)
Subfamily Stegaspidinae ² Haupt	Subfamily Stegaspidinae Haupt
Tribe Stegaspidini ³ Haupt	Tribe Stegaspidini Haupt
Bocydium Latreille (9 spp.)	Bocydium Latreille (15 spp.)
Stylocentrus Stål (3 spp.)	Stylocentrus Stål (3 spp.) ⁴
Umbelligerus, New Genus (1 sp.)	Umbelligerus Deitz (3 spp.) ⁴
Oeda Amyot and Serville (4 spp.)	Oeda Amyot and Serville (4 spp.) ⁴
Lycoderes Germar (22 spp.)	Lycoderes Germar (36 spp.) ⁴
Stegaspis Germar (10 spp.)	Stegaspis Germar (2 spp.) ⁴
Flexocentrus Goding (2 spp.)	Flexocentrus Goding (1 sp.) ⁴
Lirania Stål (1 sp.)	Lirania Stål (1 sp.)
	Smerdalea Fowler (4 spp.)
Euwalkeria Goding (1 sp.)	(Euwalkeria removed from Stegaspidini by
	Deitz and Dietrich [1993a])
	Deitz and Dietrich [1993a])

¹ Species counts based on Metcalf and Wade (1965a).

² As Stegaspinae.

³ As Stegaspini.

⁴ Discussed in Cryan and Deitz (in preparation).

Finally, independent phylogenetic analyses of morphological characters (Cryan and Deitz, in preparation; Dietrich et al., in preparation) and DNA nucleotide sequence data (Cryan and Wiegmann, in preparation) indicate that the genus *Deiroderes* Ramos is included in the subfamily Stegaspidinae. The tribal affiliation of *Deiroderes*, however, is unclear, and may even warrant a new tribe within the subfamily. Cryan and Deitz (in preparation) will present a revision of *Deiroderes* based on morphology.

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